

A new genus and two new species of deep-sea gastropods (Gastropoda: Vetigastropoda: Gazidae)

Carole S. Hickman

University of California
Department of Integrative Biology
and
Museum of Paleontology
Berkeley, CA 94720-3140 USA
earoleh@berkeley.edu

ABSTRACT

A new genus and two new species of deep-sea vetigastropod gastropods extend knowledge of the unique shell morphology, radula, anatomy, ecology, and distribution of a family group of undetermined relationship to other vetigastropods. *Anomphalogaza moluccensis* new genus and new species is the first record of the family in the Indonesian biogeographic realm of Wallacea. *Callogaza colmani* new species is the first record of the family group from the Australian Plate. Determinate growth in all known gazid species is expressed in a pronounced thickening and reflection of the final lip along with a descending suture. In the umbilicate species, determinate growth is also marked by formation of a thin reflected callus that partially or fully isolates a hollow umbilical chamber. Unique features of the Gazid radula include extremely elongated marginal teeth with strongly serrate shafts and an unusual pattern of integration in which rows of marginal tooth bases and cusps are aligned in separate rows of rachidian and lateral teeth. Distinctive anatomical features include expanded oral surface of the snout, antero-lateral extensions of the foot, and an enlarged hindgut. Numerous repaired breakages of delicate gazid shells prior to formation of the terminal lip suggest high predation pressure. Occurrences in regions of methane and sulfide seepage suggest that these relatively large deposit-feeding gastropods are nutritionally linked with unconventional carbon sources.

Original description of the family group as a tribe within Margaritinae Thiele, 1924 was based on analysis of morphological features. Subsequent molecular sequence data have shown that Margaritinae is not monophyletic, and some deep-water species described under *Margarites* Gray, 1847 may be more closely related to the gazid species described herein. Because classification of vetigastropod family group taxa is currently in a state of flux, this treatment abstains from traditional ranked classification and uses the family-group ending “-idae” in a provisional sense until complete phylogenies are available.

Additional keywords: bathyal, chemosynthesis, methane, sulfide, cold seep, Molucca Sea, Australia, deposit feeding

INTRODUCTION

Morphological support for monophyletic vetigastropod groups, including monophyletic Turbinidae and Trochidae

(Hickman and McLean, 1990; Hickman, 1996, 1998) is increasing conflict with the results of more recent molecular analyses (e.g., Geiger and Thacker, 2005; Yoon and Kim, 2005; Williams and Ozawa, 2006; Kano, 2008; Williams et al., 2008, 2010). Although monophyly of some of the morphologically based subfamilies and tribes is well supported by new genetic data, there have been some major realignments of their relationships to one another. New morphological and/or molecular data have led to a revised working classification (Bouchet and Rocroi, 2005) and redefinitions of Trochidae, Turbinidae, and Trochoidea (Williams et al., 2008).

Some of the most interesting realignments are among higher taxa restricted to habitats in the deep sea (>200 meters). Recurring features that appear to be convergent in deep-water vetigastropods include minute shell size (<5 mm), reduced shell thickness and visibility of nacre (tabular aragonite) through a thin exterior layer, extreme thinning or putative loss of nacre, secondary loss of coiling resulting in a limpet shell form, enlargement of the hindgut associated with deposit feeding, elaboration of structures for sperm transfer and sperm storage, and, in some cases, hermaphroditism.

Examples of hypothesized molecular unmasking of convergence include the recognition of two discrete clades of minute slit-shells formerly united under Scissurellidae (Geiger and Thacker, 2005) and recognition of a close relationship among minute shells of seguenziiform taxa, large- and small-shelled deep-sea trochiform taxa, and a number of minute skeneiform taxa (Kano, 2008). Taxon sampling for molecular phylogenetic analysis is still problematic and difficult for the many deep-sea taxa that are known only from shells and occasional formalin fixed specimens in wet collections.

A major gap in sampling is that of the deep-sea family-group Gazidae Hickman and McLean, 1990. Eight species in two genera, *Gaza* Watson, 1879, and *Callogaza* Dall, 1891, have many shared features (Hickman and McLean, 1990) that unite them phylogenetically (Hickman, 1996, 1998). These include shared character states for

38 of 40 radular characters (Hickman, 1996). However, the original placement of gazids as a sister group to margaritids (Hickman and McLean, 1990; Hickman, 1996) has not been tested by molecular sequence data. A recent review of *Gaza* and *Callogaza* and description of a ninth species from Brazil (Simonc and Cunha, 2006) did not address relationships, but it underscores the global distribution of the group and the potential for undocumented species.

Molecular sequence data for margaritid species resulted in a new phylogenetic hypothesis of the relationship of the family group to other vetigastropods (Williams et al., 2008). However, subsequent analyses have demonstrated that the group is not monophyletic (Williams et al., 2010). Further molecular genetic analyses are likely to alter the relationship of gazids and margaritids to each other as well as to other vetigastropods (Williams, pers. comm., 2011).

The objectives of this paper are (1) to describe a new gazid genus and two new gazid species, and (2) to provide new data highlighting the unusual features of the group, its biogeography, its ecology, and its role in the deep sea.

The family group ending -idae is used provisionally and without placing Gazidae into a ranked classification of higher taxa of vetigastropods. It does not alter its currently unresolved relationship to the family group Margaritidae, although morphological evidence is presented to suggest that some deep-water species currently assigned to Margaritidae may require re-allocation to Gazidae.

Abbreviations for specimen repositories are: AMS, Australian Museum, Sydney; LACM, Los Angeles County Museum of Natural History, Los Angeles; UCMP, University of California, Berkeley; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC.

SYSTEMATICS

Vetigastropoda (unranked)

Family Group Gazidae Hickman and McLean, 1990 (unclassified)

Genus *Callogaza* Dall, 1881

Type Species: By original designation, *Callogaza watsoni* Dall, 1881. Recent, off Havana, Cuba, 24°34' N, 83°16' W, 177 fathoms. Distribution: Northern Cuba south to Brazil, 117–500 fathoms.

Description: Shell of 1.5 smooth protoconch whorls and 6 teleoconch whorls with distinct fine spiral and axial sculpture. Smaller than *Gaza* Watson, 1879 (width < 25 mm), relatively broader, and prominently pigmented with alternating white and brown splotches or fine spiral lines on a beige background. Teleoconch whorls shouldered and finely carinate. Umbilical callus thinner than in *Gaza* and convex when completely covering umbilicus.

Callogaza colmani new species

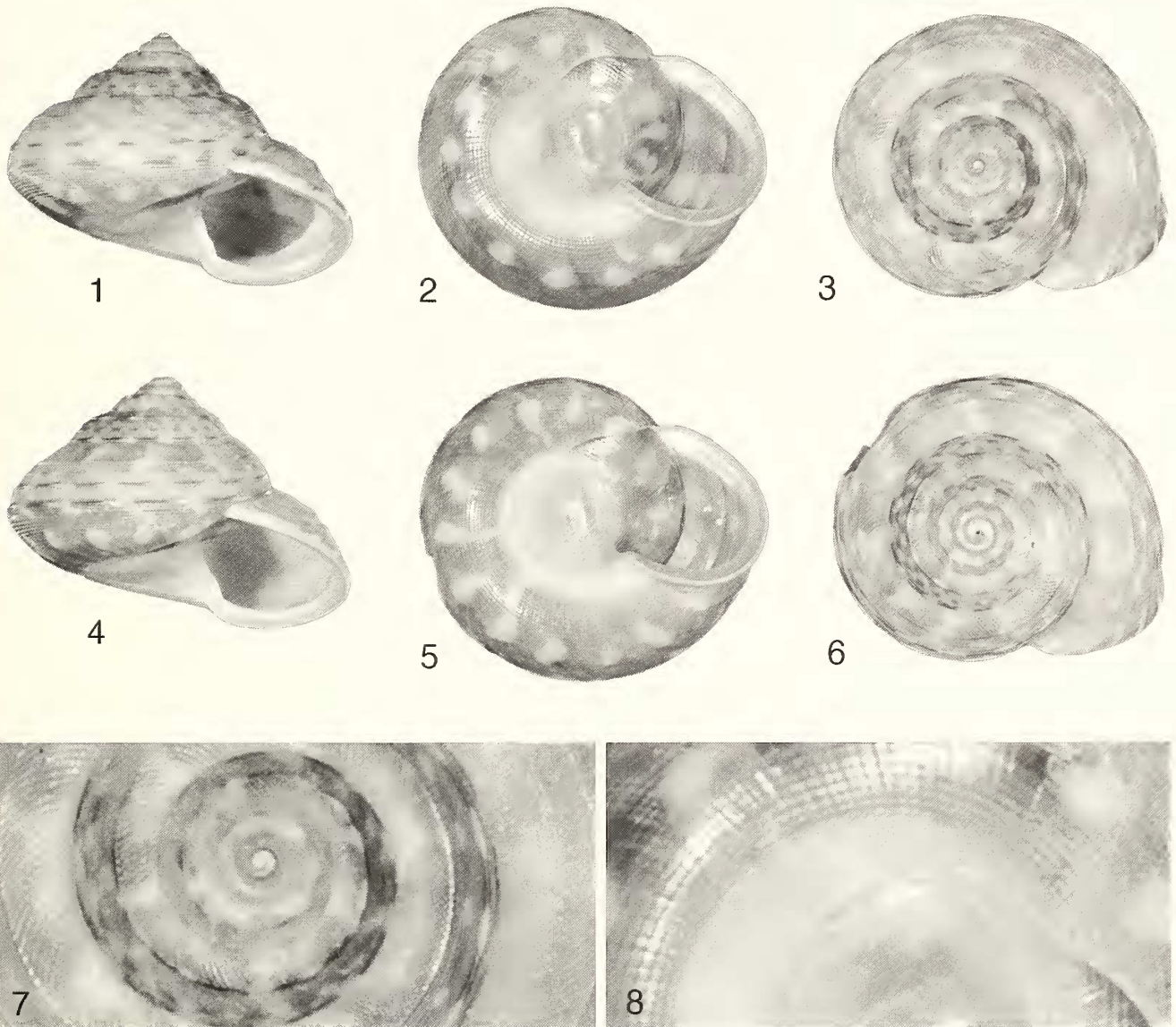
(Figures 1–10, 12, 14–15)

Gaza (*Callogaza*) sp.—Hickman and McLean, 1990, figs. 53b, c, c, f. (originally mislabeled; reported correctly here)

Description (Figures 1–8): SHELL width (up to 23.3 mm) exceeds shell height (up to 17.4 mm), and final whorl height exceeds that of spire. Aperture is strongly prosocline, inclined to axis of coiling at an angle of 50°. Terminal lip both thickened and reflected and marked by a descending suture. Thin, transparent parietal callus continuous from suture to umbilicus, where it is reflexed as a thin, slightly convex covering, creating a closed umbilical chamber. Most abapical of four spiral cords marks periphery of shell, and suture follows fourth spiral. Most apical spiral cord separates a slight shoulder from rest of whorl. On shoulder, 15 very fine spiral lines crossed by slightly stronger, finely spaced axial lines to produce a very finely cancellate surface (Figure 7). A similarly fine cancellate surface occurs between each of pairs of spirals between shoulder and periphery. There are 27 very finely incised spiral lines on base (Figure 8). Shell pigmentation consists of alternating tan and white patches on spiral ribs, with two spiral rows of prominent white blotches on base. Naere visible only through small windows of transparent shell material and only when shell is moved, generating lustrous flashes. Protoconch is small, glossy, and of 1.5 whorls.

RADULA (FIGURES 9–10, 12): Rachidian is largest tooth in central field. Rachidian tooth with broad, ovate base with triangular over-hanging cusp that emerges directly from base and is finely denticulate along both margins (Figures 9, 12). Seven pairs of lateral teeth present, also with broad bases and triangular, denticulate eusps (Figures 9, 12). Inner portion of each lateral base is obscured by overlapping base of adjacent tooth. Cusp of each lateral tooth directed toward midline, overhanging outer portion of base of adjacent lateral tooth (Figure 9). Outermost lateral teeth with elongate shafts and narrower, longer eusps increasingly curved inward toward rachidian. Between outermost lateral and marginal teeth, in position occupied by lateromarginal plate in generalized trochoidean radula, there are several irregularly-developed tooth bases that have failed to develop shafts and cusps (Hickman and McLean, 1990, Figure 53E, p. 92). Marginal teeth (Figure 10) with extremely long, well-developed shafts and long, narrow, overhanging denticulate cusps. Marginal cusp rows and base rows do not correspond (*sensu* Hickman, 1984a). Prominent serration of the marginal shafts (Figure 10) is a unique feature. Outermost marginal teeth have unusually broad shafts and cusps and may be partially or fully fused to one another (Figure 10).

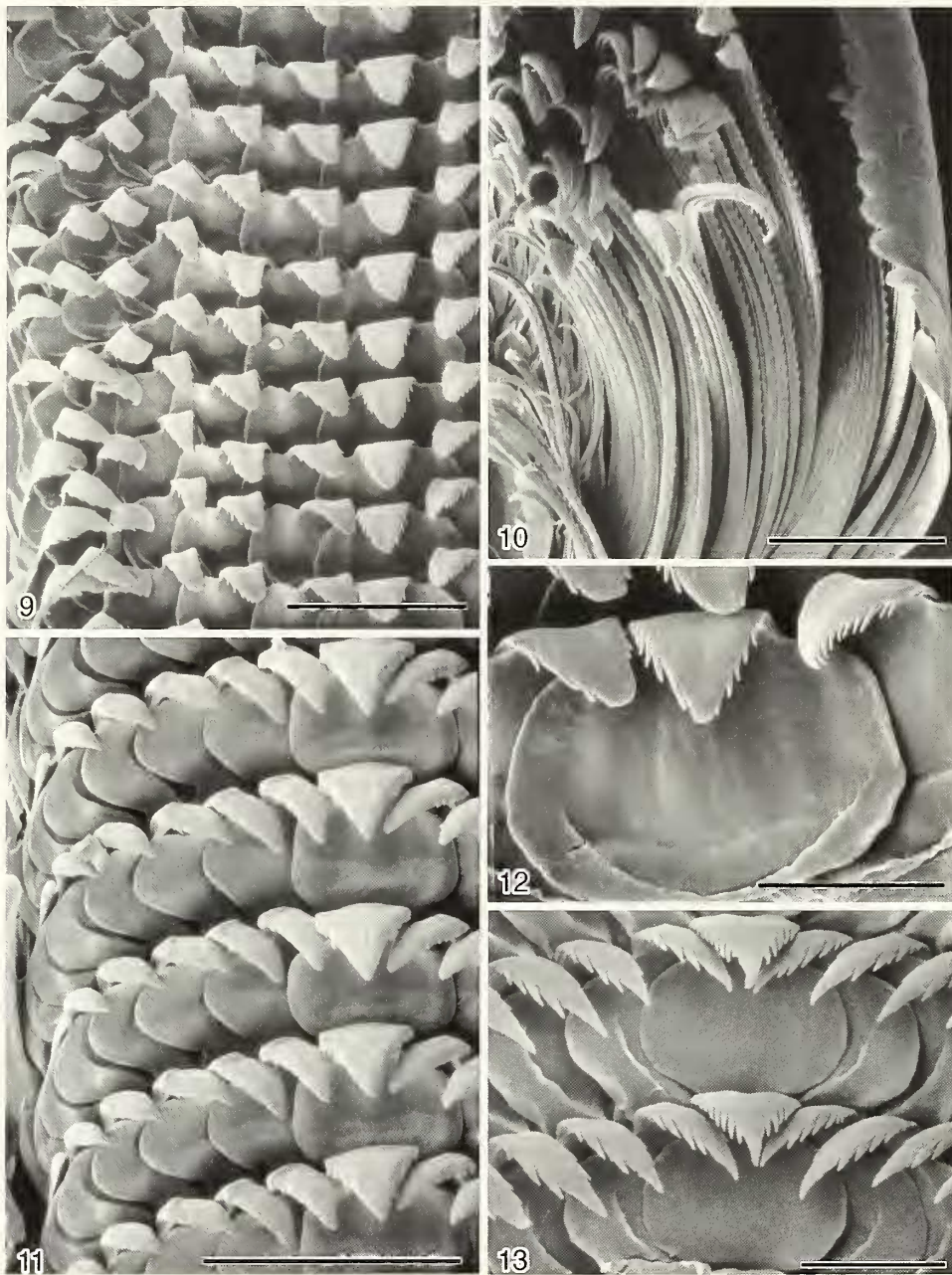
EXTERIOR ANATOMY (FIGURES 14–15): Deep transverse groove (inferred pedal gland) present along anterior margin of the propodium. In retracted and preserved animal, anterior propodium and mesopodium folded under and against sole of foot, with oral disk of snout



Figures 1–8. *Callogaza colmani* new species. 1. Apertural, 2. Basal, and 3. Apical views of the holotype, AMS 115689, height = 17.4 mm. 4. Apertural, 5. Basal, and 6. Apical views of paratype 1, AMS 115689a, height = 17.9 mm. 7. Details of sculpture on apical whorls of holotype. 8. Details of sculpture on base of holotype.

pressed against fold. Large snout cylindrical, expanding distally to a tentacular margin surrounding broad oral disc densely covered with shorter tentacles. Mouth lies within longitudinal groove on oral disc. Large, black-pigmented eyes lie at distal ends of short, thick, dorsoventrally flattened eyestalks. Inner basal margins of eyestalks continue over bases of cephalic tentacles, joining small crescent-shaped cephalic lappets. Lappets have entire margins and do not reach midline of snout. Cephalic tentacles relatively long even in their contracted state. No evidence of micropapillae on either cephalic or epipodial tentacles, but this may be a preservation artifact. Left (inhalant) and right (exhalant) neck lobes large and well-developed flaps of tissue with simple margins. Beneath each necklobe and continuing posteriorly along side of foot is a row of prom-

inent upraised papillae, six on right side and seven on left. (It is not known whether these papillae are innervated and sensory in function or glandular and secretory, although they are referred to here as epipodial sense organs. They are similar in appearance to the epipodial sense organs that are paired posteriorly with each of the epipodial tentacles.) Seven epipodial tentacles present on right side of animal and six on left. Each tentacle and its basal sense organ arise beneath a separate, thin, crescent-shaped flap of epipodial tissue. Epipodial flaps partially overlap one another in imbricate fashion. Epipodial tentacle length decreases posteriorly on both sides. On left side, anteriormost epipodial tentacle lacks a flap and basal sense organ and is longer and set apart from other five tentacles. Mantle cavity of holotype not dissected, but long free tip



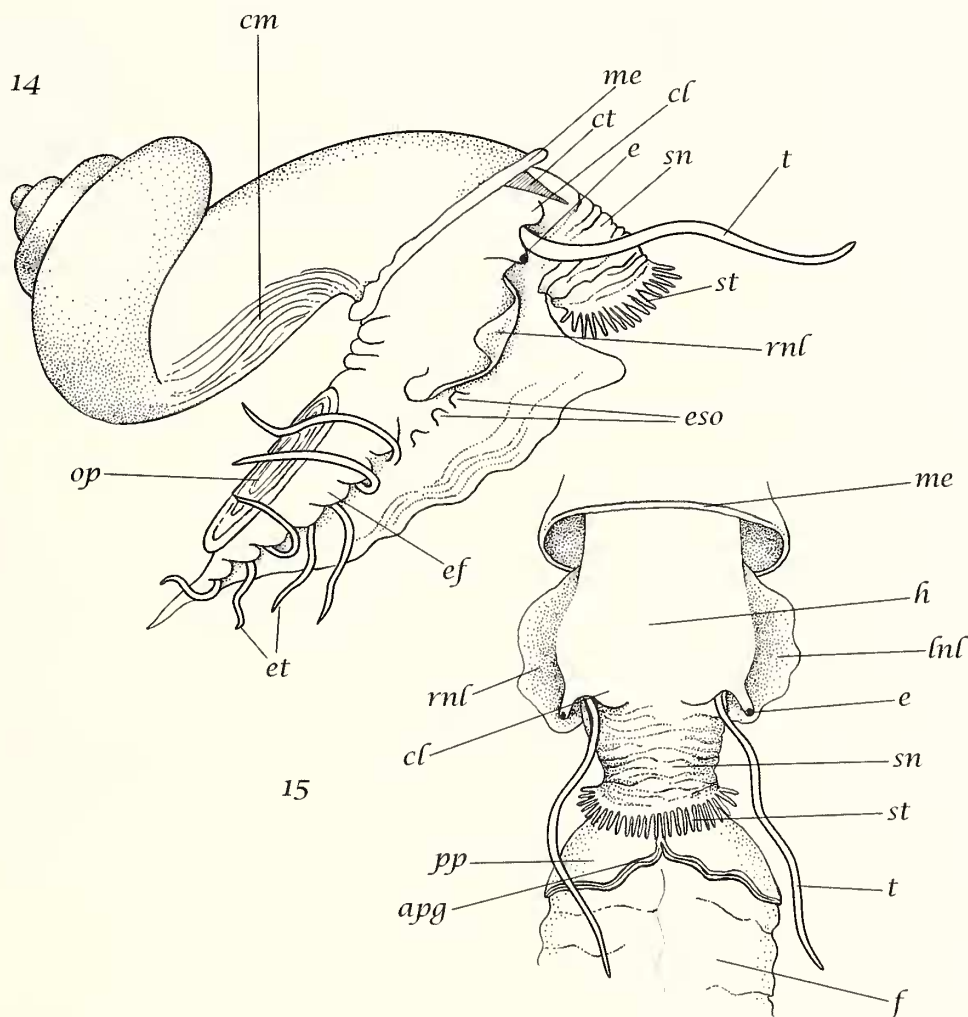
Figures 9–13. Radulae. **9–10, 12.** *Callogaza colmani* new species. **9.** Rachidian and left lateral teeth of holotype, AMS 115689, scale bar = 100 μm . **10.** Right marginal teeth of holotype, bar = 100 μm . **12.** Detail of rachidian base and serration of rachidian and inner lateral cusps of holotype, scale bar = 40 μm . **11.** Rachidian and left lateral teeth of *Gaza superba* Dall, 1881, UCMP D-3763. **13.** Rachidian and inner lateral teeth of *Margarites simbla* Dall, 1913, LACM 71-374.

of bipectinate ctenidium projects from beneath mantle margin of preserved specimen.

Remarks: The new species is distinguished from *Callogaza watsoni*, by complete nacreous terminal closure of the umbilicus and relatively higher spire. The spire is relatively lower than that of *Callogaza sericata* (Kira, 1959) from Japan, which also has a smaller shell, forming its terminal aperture at half the size of adult *C. colmani*. The Japanese species also differs in details

of spiral and axial sculpture and pigmentation pattern. Although the pigments are similar, they are distributed differently, as in the arrangement of white splotches on the base of the shell. The radula and soft anatomy are unknown for both *C. watsoni* and *C. sericata*, but the shells have been adequately figured by previous authors (see Simone and Cunha, 2006, Figures 41–48).

The shell has a relatively higher spire than the type species and a relatively lower spire than *Callogaza sericata* (Kira, 1959) from Japan. Although the Japanese species is



Figures 14–15. External anatomy of *Callogaza colmani* new species, holotype (AMS 115689) and paratype 3 (AMS 115689b). **14.** Right lateral view, **15.** Oblique view of head/foot. Abbreviations: **apg**, anterior pedal gland; **cl**, cephalic lappet; **cm**, columellar muscle; **ct**, ctenidium; **e**, eye and eyestalk; **ef**, epipodial flap; **eso**, epipodial sense organ; **et**, epipodial tentacle; **f**, foot (sole of mesopodium); **h**, head; **lnf**, left (inhalant) neck lobe; **op**, operculum; **me**, mantle edge; **p**, propodium; **rnl**, right (exhalant) neck lobe; **sn**, snout; **st**, snout tentacles; **t**, cephalic tentacle.

more similar in the pigments present in the shell, they are patterned differently, as in the arrangement of white splotches on the base of *C. sericata*. The Japanese species has a smaller shell, forming a terminal aperture at half the size of adult *C. colmani*.

This is the first account of the soft parts of *Callogaza*, and the major features link it clearly with *Gaza*. The large number of epipodial tentacles is a feature shared with some species of *Margarites* Gray, 1847, and was a significant factor in classifying *Margaritini* and *Gazini* as sister tribes by Hickman and McLean (1990). Isolated epipodial sense organs anterior to the epipodial tentacles do occur in some species of *Margarites*, although isolated papillae also occur beneath the neck lobes in a number of cantharidine gastropods (Hickman personal observation). Series of “holes” or anterior “foot orifices” illustrated in several species of *Gaza* (Simone and Cunha, 2006) are identical in placement on the foot, but

there is no evidence of holes or openings in the upraised, papillae on the foot of *Callogaza colmani*.

There is no information on the radula of other species of *Callogaza*. The radula of *C. colmani* is similar to that of *Gaza superba* (Dall, 1881) (Figure 11), although the tooth bases in the central field are thinner and the cusps are thinner and more denticulate. The large number of lateral teeth (>5 per half row) was a shared feature originally linking *Gazini* and *Margaritini* (Hickman and McLean, 1990; Hickman, 1996).

The rachidian and lateral teeth of a thin-shelled deep-water species originally described as *Margarites simbla* Dall, 1913 have many features in common with the new species of *Callogaza* and are illustrated here (Figure 13) to call attention to two eastern Pacific species that cannot be allocated at this time. The other species, *Margarites huloti* Vilvens and Sellanes, 2006, was described as part of a Chilean methane seep biota. Both species are

thin-shelled but lack gazid determinate growth features. Vilvens and Sellanes (2006) and Warén et al. (2011) compared *M. luloti* to two species described from methane seeps off Japan: *Margarites ryukyuensis* Okutani, Sasaki, and Tsuchida, 2000 and *Margarites shinkai* Okutani, Tsuchida, and Fukikura, 1992. However, both of the Japanese species have radulae with margaritid features that include the shapes of the rachidian and lateral teeth, the presence of a lateromarginal plate, and marginal teeth with base rows and cusp rows that correspond with the base and cusp rows of the central tooth complex.

Type Material: Holotype: Australian Museum, Sydney 115689 (shell and figured animal). Figured paratype 1: AMS 115689a (shell and radula). Figured paratype 2: AMS 115689b (animal). Additional paratypes: AMS 115689c–f (shells with preserved animals), Fisheries R/V KAPALA Stn. K78-23-09, 6 November 1978.

Dimensions: Holotype: height 17.4 mm, maximum width 23.3 mm. Figured paratype: height 17.9 mm, maximum width 22.9 mm.

Type Locality: Off Point Danger, New South Wales, Australia, 27°55–57' S, 154°03' E, 550 m. Point Danger is not recognized as a place name by the Australian Department of Natural Resources, Division of National Mapping. It is, however, on Admiralty Charts used by the KAPALA, and P. H. Colman (pers. comm., 2008) traces its origin to 1770 when Captain James Cook gave the name of “Mount Warning” to a prominent feature onshore and “Point Danger” to the corresponding offshore point where shoals lay. Cook further noted: “Point Danger is the boundary point on the coast between NSW and Qld.”

Distribution: The bathymetric and geographic distributions of this species are yet to be determined, but the recovery of 7 live specimens in a single dredge haul suggests that it may be locally abundant. The same haul contained three live specimens of another large-shelled vetigastropod, the calliotropid *Calliotropis glypta* (Watson, 1879).

Etymology: Named in honor of Philip H. Colman, formerly of the Australian Museum, Sydney, who was on the dredging expedition and called the material to the attention of the author.

Genus *Anomphalogaza* new genus

Type Species: *Anomphalogaza moluccensis* new species, by monotypy.

Description: Shell lacking umbilicus, shell height (up to 29.2 mm) exceeding shell width (up to 22.1 mm). Interior nacreous layer thickest, covered by two distinct, unpigmented outer layers. No evidence of opalescent sheen from underlying nacreous layer. Nacreous layer, as well as outer layers, thickened and reflexed at terminal aperture. Terminal aperture descending. Nacreous parietal callus divided into two portions, one on upper parietal wall immediately below upper termination of outer

lip and other on lowermost parietal wall and connected to columellar callus. Thin, transparent shell layer of unidentified composition superimposed as secondary callus on underlying columellar and parietal callus and continuous across parietal wall. Final whorl sculpture consisting of 130 closely-spaced, very finely-incised spiral lines crossed by fine closely-spaced collabral growth lines, visible only with magnification. Suture slightly adpressed to preceding whorl throughout coiling.

Remarks: The thickened and reflexed outer lip is a unique shared feature of all species of Gazidae. It is accompanied by a descending suture immediately prior to formation of the terminal lip. Both features are indicative of determinate growth. The thin parietal and columellar callus may also be terminal features, but younger individuals will be required to determine if this is the case.

The genus is distinguished from *Gaza* and *Callogaza* by the absence of an umbilicus by and relatively greater shell height. Height exceeds width, and the generating curve is tangent to the axis of coiling, precluding the presence of umbilical space. It is further distinguished from *Callogaza* by larger adult size (>20 mm), lack of pigmentation, and the absence both of axial sculpture and any strong spiral elements or peripheral demarcation. Shells lack the lustrous sheen typical of both *Gaza* and *Callogaza*. The suture is slightly adpressed to the preceding whorl in contrast to the impressed suture in species of *Gaza*, and the aperture is less prosocline.

The shell apex is worn on both holotype and paratype, obscuring the details of protoconch size and early teleoconch sculpture.

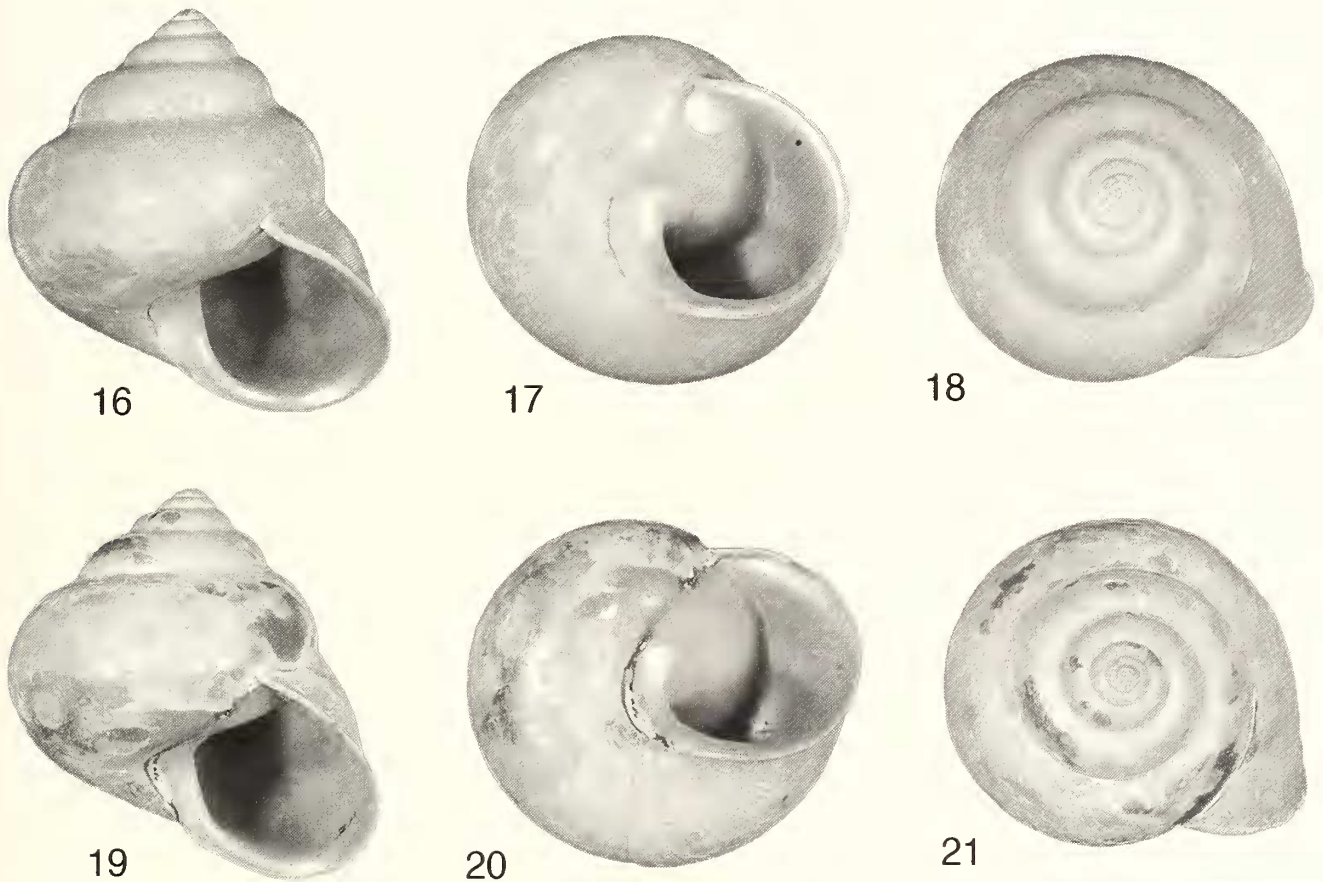
Etymology: *an* (Gr. without) + *omphalos* (Gr. umbilicus), recognizing that there is neither an open umbilicus or an umbilicus that has been sealed over by secretion of a terminal callus deposit.

Anomphalogaza moluccensis new species (Figures 16–21)

Description: Same as for genus (monotypic genus).

Remarks: The holotype and paratype were both collected as empty shells. Unlike many gazid species, the apex of the shells is not perforated and the shells are free of epi- and endobionts. However, the shell of the paratype is corroded; and the exfoliation of outer shell has exposed the evidence of two distinct layers. Both shells sustained and repaired episodes of sublethal damage to the growing margin of the aperture. On the holotype there are six repaired breakages on the body whorl and eight on the exposed portion of spire whorls. Both specimens repaired an irregular breakage along the entire apertural margin immediately prior to secretion of the terminal apertural rim.

Type Material: Holotype USNM 311367. Paratype USNM 311367b. Both empty shells.



Figures 16–21. *Anomphalogaza moluccensis* new species. **16.** Apertural, **17.** Basal, and **18.** Apical views of the holotype, USNM 311367, height = 29.2 mm. **19.** Apertural, **20.** Basal, and **21.** Apical views of paratype, USNM 311367a, height = 28.0 mm.

Dimensions: Holotype: Height 29.2 mm, maximum width 22.1 mm. Paratype: Height 28.0 mm, maximum width 21.9 mm.

Type Locality: U.S. Fish Commission, R/V ALBATROSS, Station 5601. 13 November 1909. 01°13'10" N, 125°17'05" E. Molucca Sea, Indonesia, Celebes (Sulawesi). 765 Fathoms (=1,399 m). Sand, *Globigerina* and pteropods.

Distribution: The genus and species are thus far known from only a single locality at greater depth than any of the gazid taxa described to date and in a setting that is more geologically remote and isolated. It is isolated by its tectonic setting at the western edge the Molucca Sea Microplate, the only known site of active collision between two facing Island Arcs. The geologic complexity of this region is treated further in the discussion because it is pertinent to understanding the geologic and evolutionary history of the deep-sea fauna.

DISCUSSION

BIOLOGICAL AND PALEOBIOLOGICAL REASSESSMENTS

Gaza and *Callogaza* have been recognized for many years as conspicuous elements of the tropical Western Atlantic

and Caribbean fauna (Clench and Abbott, 1943). Their relatively large shell sizes and local abundance (Quinn, 1979) have facilitated their use as models for understanding taphonomic and paleoecological phenomena in deep-sea gastropods (Walker and Voight, 1994; Voight and Walker, 1995). The *Gaza* Community was designated as an example of a deep-water community type with origins in the Eocene (Hickman, 1984b). Discoveries of chemosynthetically nourished communities in the northern Gulf of Mexico (Kennicutt et al., 1985) suggest a potentially unconventional carbon source for these large gastropods.

Four aspects of the morphology and biology of these gastropods are reconsidered here: (1) the phenomenon of determinate growth, (2) the high incidence of repair of sublethal shell damage, (3) the umbilicate condition, and (4) the nutritional carbon source.

DETERMINATE GROWTH IN GAZID GASTROPODS: Determinate growth is manifest in three morphological features of gazid gastropods: (1) reflection and thickening of the outer lip, (2) reflection of the columellar lip to form a thin callus completely or partially covering the umbilicus, and (3) a descending suture. It is the only family-group vetigastropod taxon in which all known species develop these three features. The thickened and reflected lip was

used as a diagnostic feature in proposal of the family-group name (Hickman and McLean, 1990). The thin, translucent, bubble-like callus is, likewise, a unique derived feature of the genus *Callogaza* (Hickman, 1998).

In marine gastropods, determinate growth occurs primarily in siphonate caenogastropods and in shallow-water, tropical habitats (Vermeij and Signor, 1992). It is recognized most often by a terminal elaboration of the aperture, which may be thickened, reflected, or flaired. Other signatures of cessation of spiral growth in caenogastropods include the formation of a distinctive parietal callus that may extend onto the spire and a change in the direction of spiral growth, where it is referred to as an "ascending suture" (Vermeij and Signor, 1992).

Although determinate growth has been considered rare in the basal "archaeogastropod" groups (Vermeij and Signor, 1992), there is increasing evidence of terminal features that do not occur earlier in ontogeny. In contrast to siphonate caenogastropods, changes in direction of spiral growth are typically recorded as a descending suture between the body whorl and penultimate whorl. A descending suture immediately precedes the formation of the thickened terminal lip can be seen in both the new species of *Callogaza* and the new genus *Anomphallogaza*. In other basal gastropod clades a descending suture occurs in some, but not all, species. If there is no terminal modification of the lip, a descending suture may accompany a slowing of growth in the largest individuals. For example, some species of *Clanculus* Montfort, 1810 have a descending suture without any terminal modification of the aperture (Hickman, personal observation). In contrast, a descending suture is paired with a flaired and reflexed aperture in some species of deep-water gastropods in the genus *Calliotropis* Seguenza, 1903 (Hickman, personal observation).

The descending suture forces the spire of the active crawling animal upward, increasing the angle between the axis of coiling and the substrate. Functional significance of the change in coiling geometry is not known, nor is the function of terminal modification of the aperture. Walker and Voight (1994) reported high shell repair frequency in two species of *Gaza* in a study showing that attempted predation is common in large-shelled (>25 mm height) gastropods, although rare in small-shelled species. If the ability to repair apertural damage decreases with age, formation of a thickened terminal aperture may provide an adaptive advantage to reproductively mature adults. Irregular breakages on the shells of *Gaza superba* indicate that there was no terminal thickening at the time the damage occurred.

SHELL REPAIR IN GAZID GASTROPODS: High frequency of shell repair in living and fossil marine gastropods serves as an indicator of predation pressure and of predator ability to survive attempted predation (Vermeij, 1982). Studies of shell repair frequencies on small-shelled gastropods concluded that predation pressure was low in the deep sea (Vale and Rex, 1988, 1989). It is therefore surprising that later studies of large-shelled deep-sea

gastropods not only show high repair frequencies but also that the shells of these species lack the typical anti-predator adaptations (Walker and Voight, 1994; Harasewych, 2002). A study of repaired breakage in pleurotomariid gastropods reported "extraordinarily high level of unsuccessful predation for all species examined" (Harasewych, 2002). This is surprising because these species have an uncalcified operculum, relatively thin shell, and open umbilicus that should render them mechanically more vulnerable than taxa with robust shells, no umbilicus, and a heavy calcareous operculum. However, living pleurotomariids also appear to be well defended chemically by a hypobranchial gland secretion that is released in response to disturbance and shell damage (Harasewych, 2002). High shell repair frequencies were also reported in a study of species of *Gaza* and large-shelled species of the calliotropid genus *Bathybembix* Crosse, 1893 (Walker and Voight, 1994).

THE UMBILICATE CONDITION IN GAZID GASTROPODS: The terms used to describe the umbilicate condition in gastropods are difficult to apply to gazids because closure of an umbilical opening, if it occurs, is a thin reflected nacreous layer secreted at the cessation of growth. The shell is phanerocephalous until growth ceases and never becomes partially or completely plugged in the sense of hemiophalous or cryptophalous. The terminal partial or complete sealing off of the umbilicus partially or completely hides its presence as an empty chamber.

In the new genus *Anomphallogaza*, there simply is no umbilicus, and the terminal columellar and parietal calluses are reflected over shell only: there is no opening to seal off.

The lack of an umbilical plug contributes to the lightness of the shell and low investment in calcium carbonate. The perforation of the apex in some species, rendering the umbilicus open at both ends, is permitted by the lack of filling. The lack of umbilical filling has permitted use of the umbilicus of *Gaza superba* and *Gaza olivacea* Quinn, 1981 by a polychaete that is alleged to create the apical perforation (Quinn, 1991; Voight and Walker, 1995).

NUTRITIONAL CARBON SOURCE OF GAZID GASTROPODS: *Gaza* and *Callogaza* have not been identified conclusively as elements of chemosynthetically nourished communities. However, *Gaza superba* and *Gaza fischeri* Dall, 1889 are locally abundant on the upper slope in the Gulf of Mexico in regions of confirmed methane and sulfide seepage (Kennicutt et al., 1985; Carney, 1994). Five new records of *Gaza fischeri* from the Louisiana slope are included in an account of seep and vent gastropods (Warén and Bouchet, 1993). There is no evidence of an enriched photosynthetically derived (detrital) carbon source to support communities dominated by gazid species. However, the alternative possibility of diffuse seepage (*sensu* Nesbitt and Campbell, 2004) supporting chemoautotrophic bacterial synthesis of organic carbon in and on the sediments is worth investigating. Possible sources of enriched dietary carbon also include bacterial degradation of hydrocarbons in sediments (Brooks et al.,

1987). In this instance, the concept of a seep community is not synonymous with chemosymbiosis. It is, however, indicative of an unconventional carbon source.

The enlarged hindguts of these gastropods are packed with sediment, and sedimentary grain coatings have been implicated as a significant source of nutrition for large deposit-feeding gastropods that selectively ingest grains with the greatest surface area to volume ratio (Hickman, 1981). The earliest occurrences (late Eocene) of large-shelled calliotropid gastropods of the genus *Bathybembix* are in a geological setting of both discrete and diffuse methane seepage on an active continental margin (Hickman, 2003).

BIOGEOGRAPHIC REASSESSMENT

The new taxa described here call attention to a more global biogeographic pattern and to extra-tropical occurrences in the Western Pacific. *Callogaza colmani* is the first representative of the family recognized from the Australian plate with its Gondwanan origin and history. *Anomphalogaza mohuccensis* is the first gazid described from the biogeographic region of Wallacea. Indonesia as political and modern geographic unit has been assembled over the past 55 million years from complex tectonic evolution of major plate boundaries and microplates. In the Eocene, present day Sulawesi (although not emergent as land) was situated south of Borneo and west of its present location in eastern Indonesia (Hall, 2001). The type locality for the new gazid genus and species is on the disappearing western boundary of what was once a large sea. The ancient Molucca Sea has been squeezed and subducted by convergence of the Philippine Sea Plate, the Australian Plate, and the Eurasian Plate (Widwijayanti et al., 2003). The disappearance of the Molucca Sea has received considerable attention because it is the only present-day example of active collision between two facing volcanic arc-trench systems. Subduction beneath Halmahera to the east and beneath Sulawesi to the west is consuming the last of the microplate (McCaffery et al., 1980; Hall et al., 1995; Hall, 2000). The thick, deformed seafloor collision complex trapped between north arm of Sulawesi and Halmahera is, at minimum, only 250 km in width (McCaffery et al., 1980). The potential marine biogeographic importance of this complex history is that the shrinking ocean basin in which *Anomphalogaza* occurs will have disappeared in another three million years (Hickman, 2009).

The northern Arm of Sulawesi, the Molucca Sea, and Halmahera are situated at the northern edge of the biogeographic region of Wallacea in the region of least distance between Wallace's Line and Lydekker's Line. The sharp terrestrial biogeographic breaks that define Wallacea have been considered invisible to shallow marine taxa, although there are recent challenges that suggest a "marine Wallace's line" (Barber et al., 2000). For the deep-water fauna, the concept of Wallacea requires greater attention to structural features, tectonics,

and longer geologic history (see Lee and McCabe, 1986). With the knowledge that active plate margins are sites of venting and seepage fueling chemosynthetically based communities, it is now possible to target sites that have never been sampled for chemosymbiotic taxa in the waters of Southeast Asia and the SW Pacific.

FUTURE DIRECTIONS

New morphological and anatomical data from this report, combined with detailed anatomical data from a new Brazilian species (Simone and Cunha, 2006) are consistent with previous morphological inference of gazid monophyly, regardless of rank and classification. The novel combination of features of shell, radula, anatomy, nutrition, and ecology distinguish it from other vetigastropod family groups. However, the relationships of family groups of vetigastropods are still poorly resolved, and morphological data presented here do not address phylogenetic relationships. For the morphologist, the challenge lies in unmasking convergence.

Strong morphological convergence in deep-sea vetigastropods is clearly related to deep-sea benthic ecology and deposit-feeding (Hickman, 1981, 1984b, 2003). The enlarged hindgut, expanded and tentacular oral disk margin, and anteriolateral expansion of the foot also occur in large, deposit-feeding seguenzioid gastropods such as species of *Bathybembix* Crosse, 1893 and *Calliotropis* Seguenza, 1903, a genus that is unusually abundant and speciose at bathyal depths throughout the world and especially in the Indo-Pacific (Vilvens, 2007). Shells also have converged on visibility of nacre through an extremely thin outer shell layer and terminal growth features that include flaring or thickening of the terminal aperture, a descending suture, and reflection of the columellar callus to partially or fully cover (but not fill) the umbilicus (Hickman, personal observation).

Thinning of the shell and terminal growth features are also common convergent shell features in several deep-water skeneiform gastropod groups (Hickman, personal observation). In describing the enigmatic Australasian family group Kaiparathini (under Margaritinae), Marshall (1993), noted several anatomical similarities to *Gaza superba*. Kaiparathinids do not fit comfortably into existing vetigastropod classification.

The genus *Margarites* Gray, 1847 needs both morphological and molecular work to identify taxa that belong elsewhere. More than 50 species have been assigned to the genus. In addition to the deep-water species noted above as candidates for transfer to Gazidae, there are extinct deep-water species dating back to the Cretaceous. Kaim et al. (2009) described *Margarites sasakii* from a Campanian cold seep site in northern Hokkaido, Japan, indicating deep origins of vetigastropods in chemosynthetically based communities. Deep-water fossil species are also described from Eocene cold-seep carbonates in Paleogene rocks in the Pacific Northwest (e.g. Squires and Goedert, 1991).

ACKNOWLEDGMENTS

This paper is part of a project begun in 1975 to document new taxa of deep-water vetigastropods. I am grateful to Jerry Harasewych and the late Joe Rosewater for their assistance and encouragement in the use of material from the Smithsonian Institution and to Winston Ponder, Phil Colman, and Ian Loch of the Australian Museum, Sydney for assistance in the study of Australian material. I am grateful to Jim Quinn, Bruce Marshall, and Dai Herbert, and Jim McLean for earlier discussions of trochoidean morphology and relationships. Sally Walker and Geerat Vermeij have contributed to my interest in *Gaza* and its allies through their fascination with unsuccessful predation, shell repair, and the phenomenon of determinate growth in gastropods. Discussions with Suzanne Williams have been especially helpful in considering the alternative approaches to vetigastropod taxonomy, phylogeny, and achievement of stability in classification. I thank Jerry Harasewych and an anonymous reviewer for helpful suggestions for improvement of the manuscript. Marla Coppolino rendered the anatomical drawings.

LITERATURE CITED

- Barber, P.H., S.R. Palumbi, M.V. Erdmann, and M.K. Moosa. 2000. A marine Wallace's line? *Nature* 406: 692–693.
- Bouchet, P. and J.-P. Rocroi, (eds.). 2005. Classification and Nomenclator of Gastropod Families. *Malacologia* 47: 1–397.
- Brooks, J.M., M.C. Kennicutt II, C.R. Fisher, S.A. Macko, K. Cole, J.J. Childress, R.R. Bidigare, and R.D. Vetter. 1987. Deep-sea hydrocarbon seep communities: evidence for energy and nutritional carbon sources. *Science* 238: 1138–1142.
- Carney, R.S. 1994. Consideration of the oasis analogy for chemosynthetic communities at Gulf of Mexico hydrocarbon vents. *Geo-Marine Letters* 14: 149–159.
- Clench, W.J. and R.T. Abbott. 1943. The genera *Gaza* and *Livona* in the Western Atlantic. *Johnsonia* 12: 1–12.
- Geiger, D.L. and C.E. Thacker. 2005. Molecular phylogeny of Vetigastropods reveals non-monophyletic Scissurellidae, Trochoidea, Fissurelloidea. *Molluscan Research* 25: 47–55.
- Hall, R. 2000. Neogene history of collision in the Halmahera region, Indonesia. Proceedings of the Indonesian Petroleum Association, 27th Annual Convention, pp. 487–493.
- Hall, R. 2001. Cenozoic reconstructions of Southeast Asia and the SW Pacific: changing patterns of land and sea. In: L. Metcalfe, J.M.B. Smith, M. Morwood and I.D. Davidson (eds.) *Faunal and Floral Migrations and Evolution in SE Asia-Australasia*. A.A. Baklkema, Lisse, pp. 35–56.
- Hall, R., J.R. Ali, C.D. Anderson, and S.J. Baker. 1995. Origin and motion history of the Philippine Sea Plate. *Tectonophysics* 251: 229–250.
- Harasewych, M.G. 2002. Pleurotomarioidean gastropods. *Advances in Marine Biology* 42: 237–295.
- Hickman, C.S. 1981. Selective deposit feeding by the deep-sea archaeogastropod *Bathybembix acola*. *Marine Ecology Progress Series* 7: 339–342.
- Hickman, C.S. 1984a. Implications of radular tooth-row functional integration for archaeogastropod systematics. *The Veliger* 26(2): 189–194.
- Hickman, C.S. 1984b. Composition, structure, ecology, and evolution of six Cenozoic deep-water mollusk communities. *Journal of Paleontology* 58: 1215–1234.
- Hickman, C.S. 1996. Phylogeny and patterns of evolutionary radiation in trochoidean gastropods. In: J.D. Taylor (ed.) *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press, Oxford, pp. 177–198.
- Hickman, C.S. 1998. Subfamily Margaritinae. In: P.L. Beesley, G.J.B. Ross and A. Wells (eds.) *Mollusca: the Southern Synthesis. Fauna of Australia*, V. 5, CSIRO Publishing: Melbourne, Part B, viii, pp. 682–683.
- Hickman, C.S. 2003. Evidence for abrupt Eocene-Oligocene molluscan faunal change in the Pacific Northwest. In: D.R. Prothero, E.A. Nesbitt and L. Ivany (eds.) *From Greenhouse to Icehouse: The Marine Eocene-Oligocene Transition*. Columbia University Press, New York, pp. 71–87.
- Hickman, C.S. 2009. Relict deep-water gastropods in a disappearing seaway. Program and Abstracts – American Malacological Society 75th Annual Meeting. Paleontological Research Institution Special Publication 37: 45.
- Hickman, C.S. and J.H. McLean. 1990. Systematic revision and suprageneric classification of trochacean gastropods. *Natural History Museum of Los Angeles County Science Series* 35: 1–69.
- Kaim, A., R.G. Jenkins, and Y. Hikida. 2009. Gastropods from Late Cretaceous Omagari and Yasukawa hydrocarbon seep deposits in the Nakagawa area, Hokkaido, Japan. *Acta Palaeontologica Polonica* 54(3): 463–490.
- Kano, Y. 2008. Vetigastropod phylogeny and a new concept of Seguenzioidea: independent evolution of copulatory organs in the deep-sea habitats. *Zoologica Scripta* 37: 1–21.
- Lee, C.S. and R. McCabe. 1986. The Banda-Celebes-Sulu basin: a trapped piece of Cretaceous-Eocene oceanic crust? *Nature* 332: 51–54.
- Kennicutt, M.C., II, J.M. Brooks, R.R. Bidigare, R.R. Fay, T.L. Wade, and T.J. McDonald. 1985. Vent-type taxa in a hydrocarbon seep region on the Louisiana slope. *Nature* 317: 351–353.
- McCaffrey, R., E.A. Silver, and R. Raitt. 1980. Crustal structure of the Molucca Sea collision zone, Indonesia. In: D.E. Hayes (ed.) *The Tectonic and Geological Evolution of Southeast Asian Seas and Islands*. American Geophysical Union Geophysical Monograph 23: 161–177.
- Marshall, B.A. 1993. A review of the genus *Kaiparathina* Laws, 1941 (Mollusca: Gastropoda: Trochoidea). *The Veliger* 36: 185–198.
- Nesbitt, L.A. and K.A. Campbell. 2004. Spatial and stratigraphic distribution of fossils from diffuse seeps in a Pliocene shelf setting, Cascadia convergent margin. *Geological Society of America Abstracts with Programs* 36(5): 314.
- Quinn, J.F., Jr. 1979. Biological results of the University of Miami Deep-sea expeditions. 130. The systematics and zoogeography of the gastropod family Trochidae collected in the Straits of Florida and its approaches. *Malacologia* 19: 1–62.
- Quinn, J.F., Jr. 1991. New species of *Gaza*, *Mirachelus*, *Calliotropis*, and *Echinogurges* (Gastropoda: Trochidae) from the Northwestern Atlantic Ocean. *The Nautilus* 105: 166–172.
- Simone, L.R.L. and C.M. Cunha. 2006. Revision of genera *Gaza* and *Callogaza* (Vetigastropoda, Trochidae) with description of a new Brazilian species. *Zootaxa* 1381: 1–40.
- Squires, R.L. and J.L. Goedert. 1991. New late Eocene mollusks from localized deposits formed by subduction-related

- methane seeps, southwestern Washington. *Journal of Paleontology* 65: 412–416.
- Vale, F.K. and M.A. Rex. 1988. Repaired shell damage in the deepsea prosobranch gastropods from the western north Atlantic. *Malacologia* 28: 65–79.
- Vale, F.K. and M.A. Rex. 1989. Repaired shell damage in a complex of rissoid gastropods from the upper continental shelf south of New England. *Nautilus* 103: 105–108.
- Vermeij, G.J. 1982. Gastropod shell form, breakage and repair in relation to predation by the crab *Calappa*. *Malacologia* 231: 1–12.
- Vermeij, G.J. and P.W. Signor. 1992. The geographic, taxonomic and temporal distribution of determinate growth in marine gastropods. *Biological Journal of the Linnean Society* 47: 233–247.
- Vilvens, C. 2007. New species and new records of *Calliotropis* (Gastropoda: Chilodontidae: Calliotropinae) from Indo-Pacific. *Novapex* 5: 1–72.
- Vilvens, C. and J. Sellanes. 2006. Descriptions of *Otukaia crustulum* new species (Gastropoda: Trochoidea: Calliostomatidae) and *Margarites huloti* new species (Gastropoda: Trochoidea: Trochidae) from a methane seep area off Chile. *The Nautilus* 120: 15–20.
- Voight, J.R. and S.E. Walker. 1995. Geographic variation of shell bionts in the deep-sea snail *Gaza*. *Deep Sea Research* 42: 1261–1271.
- Warén, A. and P. Bouchet. 1993. New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. *Zoological Scripta* 22: 1–90.
- Warén, A., T. Nakano, and J. Sellanes. 2011. A new species of *Iothia* (Gastropoda: Lcpetidae) from Chilean methane seeps, with comments on the accompanying gastropod fauna. *Nautilus* 125: 1–14.
- Walker, S.E. and J.R. Voight. 1994. Paleoecologic and taphonomic potential of deep-sea gastropods. *Palaios* 9: 48–59.
- Widiwijayanti, C., V. Mikhailov, M. Diament, C. Dephus, R. Louat, S. Tikhotsky, and A. Gvishiani. 2003. Structure and evolution of the Molucca Sea area: constraints based on interpretation of a combined sea-surface and satellite gravity dataset. *Earth and Planetary Science Letters* 215: 135–150.
- Williams, S.T. and T. Ozawa. 2006. Molecular phylogeny suggests polyphyly of both the turban shells (Family Turbinidae) and the superfamily Trochoidea (Mollusca: Vetigastropoda). *Molecular Phylogenetics and Evolution* 39: 33–51.
- Williams, S.T., S. Karube, and T. Ozawa. 2008. Molecular systematics of Vetigastropoda: Trochidae, Turbinidae and Trochoidea redefined. *Zoologica Scripta* 37: 483–506.
- Williams, S.T., K.M. Donald, H.G. Spencer, and T. Nakano. 2010. Molecular systematics of the marine gastropod families Trochidae and Calliostomatidae (Mollusca: Superfamily Trochoidea). *Molecular Phylogenetics and Evolution* 54: 783–809.
- Yoon, S.K. and W. Kim. 2005. Phylogenetic relationships among six vetigastropod groups (Mollusca, Gastropoda) based on 18S rDNA sequences. *Molecules and Cells* 19: 283–288.